RESEARCH ARTICLE

Hadronotus pubescens (Motschoulsky) (Hymenoptera, Scelionidae): Redescription, biological attributes, and parasitism on eggs of *Riptortus pedestris* (Fab.) (Hemiptera, Alydidae)

Md. Rasel Raju[1], Mst. Arifunnahar[1], Md. Munir Mostafiz[2],
Md. Abdul Alim[1], Md. Alamgir Hossain[1], Elijah J. Talamas[3]

1 *Department of Entomology, Hajee Mohammad Danesh Science and Technology University, Dinajpur-5200, Bangladesh* **2** *Division of Applied Biosciences, College of Agriculture and Life Sciences, Kyungpook National University, Daegu, 41566, Republic of Korea* **3** *Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA*

Corresponding authors: Md. Abdul Alim (alim@hstu.ac.bd), Elijah J. Talamas (elijah.talamas@fdacs.gov)

Citation: Raju MdR, Arifunnahar M, Mostafiz MdM, Alim MdA, Hossain MdA, Talamas EJ (2022) *Hadronotus pubescens* (Motschoulsky) (Hymenoptera, Scelionidae): Redescription, biological attributes, and parasitism on eggs of *Riptortus pedestris* (Fab.) (Hemiptera, Alydidae). Journal of Hymenoptera Research 94: 139–161. https://doi.org/10.3897/jhr.94.93512

Abstract

Riptortus pedestris (Fab.) (Hemiptera, Alydidae) is one of the most damaging insects of leguminous crops in Eastern Asia but has only recently emerged as a pest in Bangladesh. Eggs, nymphs and adults of *R. pedestris* are here reported from mung bean (*Vigna radiata* (L.)) fields in Bangladesh. Two parasitoid species were reared from field-collected eggs of *R. pedestris*, the solitary *Hadronotus pubescens* (Motschoulsky) (Hymenoptera, Scelionidae) and a gregarious species of *Ooencyrtus* Ashmead (Hymenoptera, Encyrtidae). Here we redescribe *H. pubescens*, treat *H. hogenakalensis* (Sharma) as a junior synonym, and report aspects of its biology that were investigated under laboratory conditions. The number of eggs parasitized by *H. pubescens* was constant with eggs up to 48 hours in age, decreasing by 14% for 96 hour-old eggs. As host egg age increased, the parasitoid mean development time increased and the longevity of the parasitoids decreased.

Keywords

Introduction

Riptortus pedestris (Fab.) (Hemiptera, Alydidae) is a destructive pest on a wide range of crop plants in Korea and Japan (Honda 1986; Son et al. 2000; Kang et al. 2003; Lee et al. 2004) and has infested many leguminous crops in Bangladesh (Arifunnahar et al. 2019, 2021). It is also an important hemipteran pest of soybean (*Glycine max* (L.) Merr.) (Osakabe and Honda 2002; Choi et al. 2005) and fruit trees (Chung et al. 1995). *Riptortus pedestris* is a major pest of many grains, including sorghum (*Sorghum bicolor* (L.) Moench), foxtail millet (*Setaria italica* (L.) P. Beauvois), and barley (*Hordeum vulgare* L.) in the reproductive stages (Chung et al. 1995; Mainali et al. 2014), as well as other field crops in Asian countries (Kang et al. 2003; Wada et al. 2006). Nymphs and adults of *R. pedestris* feed preferentially on seeds by piercing and sucking (Choi et al. 2005). Their polyphagous nature, as well as the preferential feeding on seeds, make crop plants highly vulnerable to damage (Choi et al. 2005). Both adults and nymphs feed on the fluids from seed pods, causing them to fail to mature, turn brown, shrivel and die. Generally, when such pods are opened, the seeds inside are shriveled, undersized, or malformed. These unhealthy seeds often succumb to secondary fungal infections like yeast-spot disease (*Eremothecuim coryli* (Peglion) Kurtzman) (Kimura et al. 2008) which can lead to the complete abortion of seeds in the entire field (Li et al. 2019). Many legume growers spray insecticides to control *R. pedestris*, but this is not economically effective with mung bean (*Vigna radiata* (L.)) in Bangladesh due to its relatively low cash value. Chemical insecticides are a useful component of integrated pest management (IPM) systems when they are quick and easy to apply, economically viable, and have reliable effectiveness against the targeted insect pest (Endo and Tsurumachi 2001). However chemical insecticides often negatively impact natural enemies and may cause pest resurgence and other environmental side effects (Schwab et al. 1995). Therefore, chemical insecticides may not be economically feasible due to the higher cost of production and environmental concerns. While most chemical insecticides are fast-acting, the high mobility of these insects makes them difficult to control (Choi et al. 2005; Wada et al. 2006). In light of these difficulties, cultural practices such as delayed seeding and use of resistant varieties have been suggested for the management of various stink bugs (Bowers 1990; Wada et al. 2006). Biological control has been successfully employed against various stink bugs by introduction or augmentation of egg parasitoids (Weber et al. 1996; Orr 1998; Alim and Lim 2011) and may be an option for *R. pedestris* in Bangladesh.

Previously reported parasitoids of *R. pedestris* eggs in soybean fields in east Asia include *Hadronotus japonicus* (Ashmead) (reported as *Gryon japonicum* (Ashmead)), *Hadronotus nigricornis* (Dodd) (reported as *Gryon nigricorne* (Dodd)) (Hymenoptera, Scelionidae) and *Ooencyrtus nezarae* Ishii (Hymenoptera, Encyrtidae) (Noda 1989; Hirose et al. 1996; Mizutani et al. 1996; Son et al. 2009). Species of *Hadronotus* Förster are known to parasitize the eggs of hemipteran pests, including pentatomids such as

Piezodorus hybneri (Gmelin), *Dolycoris baccarum* (L.), *Nezara antennata* Scott and *Halyomorpha halys* (Stål) (Hirose et al. 1996; Mizutani et al. 1996; Zhang et al. 2005). However, the effective use of *Hadronotus* species for biological control requires the ability to accurately identify them. In many cases, this involves time-consuming taxonomic research, creating delays for field and laboratory studies and the publication of their results. Some recent advances in the taxonomy of the group include the work of Komeda et al. (2020), who revised some species-groups in Japan, and Talamas et al. (2021), who resurrected *Hadronotus* and provided images for many primary types of *Gryon* Haliday and *Hadronotus*.

Hadronotus pubescens is a solitary egg parasitoid reported from Sri Lanka and India, especially Karnataka (Sharma et al. 1982), but not previously recorded in Bangladesh. The biological parameters of this parasitoid are largely unknown, and to date no research on either *H. pubescens* or the egg parasitoids of *R. pedestris* has been conducted in Bangladesh. In this study, biological parameters of *H. pubescens* on *R. pedestris* eggs were evaluated in laboratory conditions to determine the parasitoid's potential as a biological control agent. These parameters included emergence rate, development time, sex ratio, adult longevity and size variation of the adult wasps.

Materials and methods

Experiments were conducted in the laboratory of the Department of Entomology, Hajee Mohammad Danesh Science and Technology University (HSTU), Dinajpur and different mung bean fields near HSTU campus from December 2019 to June 2020. The taxonomic portion of the study was conducted at the Florida State Collection of Arthropods, Gainesville, Florida, USA.

Imaging

Photographs were captured using a Macropod Microkit (Macroscopic Solutions) imaging system and rendered with Helicon Focus. In some cases, multiple images were stitched together in Photoshop to produce larger images at high resolution and magnification. Dissections for scanning electron microscopy were performed with a minuten probe and forceps. Body parts were mounted to a 12 mm slotted aluminum mounting stub using a carbon adhesive tab and sputter coated with approximately 70 nm of gold/palladium using a Denton IV sputter coater. Micrographs were captured using a Phenom XL G2 Desktop SEM.

Morphological terms

Terminology for carinae on the posterior head follows Mineo (1980) and for other characters follows Mikó et al. (2007), Lahey et al. (2021) and Talamas et al. (2021).

Abbreviations and characters annotated in the figures

atc acetabular carina (Fig. 9)
ec epiclypeal carina (Figs 2, 6)
hoc hyperoccipital carina (Fig. 4)
mc mesopleural carina (Fig. 9)
mac median carina on the vertex (Fig. 4)
mhp mesoscutal humeral pit (Fig. 10)
oc occipital carina (Fig. 4);
spf sulcus of the propodeal foramen (Fig. 11)
tcmd transverse carina of the metasomal depression (Fig. 11)
tsmd transverse sulcus of the metasomal depression (Fig. 11)
vplc ventral mesopleural carina (Fig. 9)
vprc ventral propodeal carina (Fig. 11)

Collections

Specimens on which this work is based are deposited in the following repositories with abbreviations used in the text:

FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA
SAMC Iziko Museums of South Africa, Cape Town, South Africa
USNM National Museum of Natural History, Washington, District of Columbia, USA
ZMMU Zoological Museum of Lomonosov Moscow State University, Moscow, Russia

Data deposition

The data associated with the specimens in this study are deposited at mbd-db.osu.edu and are retrievable via the collecting unit identifier (CUID) for each specimen. Images of the holotype specimens of *Muscidea pubescens* Motschoulsky and *Gryon hogenakalensis* Sharma were made available by Talamas et al. (2021) and Talamas et al. (2017), respectively, and direct links to these images are provided in the species treatment.

DNA barcoding

Genomic DNA was nondestructively isolated from whole specimens using the Qiagen DNeasy kit (Hilden, Germany) as described by Giantsis et al. (2016). PCRs were carried out to amplify the DNA barcode region of the cytochrome oxidase subunit I (COI) using the LCO/HCO primers of Folmer et al. (1994). The PCRs were performed in a 25 μL reaction volume using the KAPA HiFi Hotstart Ready Mix (Roche) per the manufacturer's standard protocol. PCR conditions were as follows: 95 °C for 2 min, followed by 32 cycles of 95 °C for 30 s, 50 °C for 40 seconds, 72 °C for 1 min with a final extension at 72 °C for 7 min. The fragments to be amplified by PCR were

separated by electrophoresis on 1.5% agarose gels. After verification, the samples were sequenced at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, Florida. GenBank accession numbers for the newly generated barcodes for *H. pubescens* and sequences from Talamas et al. (2021) are listed in Table 2.

Rearing of *R. pedestris*

Adults of *Riptortus pedestris* were collected from infested country bean (*Lablab purpureus* L.) fields near the HSTU campus during 2019 and the colony was maintained in the laboratory as described by Alim and Lim (2009). Briefly, the nymphs and adults were kept in acrylic cages (40 L × 40 W × 40 H cm), each with windows on three lateral sides covered with mesh screens for ventilation. The insects were reared at a constant temperature (30 °C ± 2) and relative humidity 75% ± 4 and with a natural photoperiod. Temperature and relative humidity were monitored by the Hydro-thermometer (HTC-1). Ascorbic acid was dissolved in water and provided to the adult *R. pedestris* in dishes along with soybean seeds. Nymphs were fed with soybean seeds and bean plants with cotyledonous leaves. Oviposition substrates were prepared by placing a few pieces of gauze fabric in the top and bottom corners inside the adult cages. The gauze was replaced every day and the eggs were collected to continue the colony. The cage was cleaned two times per week.

Rearing of *H. pubescens*

Hadronotus pubescens were reared from field-collected eggs of *R. pedestris* from country bean fields. The parasitoids were reared under laboratory conditions as described in the previous section. The males and females of *H. pubescens* were placed into plastic centrifuge tubes (50 mL) (SPL Life Sciences Co. Ltd, Korea) and provided with honey on the inner surface of the tube and a piece of moistened cotton. Moistened cotton and honey were replaced every three days.

Abundance of *R. pedestris* and its egg parasitoids at different locations

To determine the parasitism rate of field-laid eggs, 10 mung bean plants were randomly selected in plots at three locations (Table 1). These plants were examined every 10 days from February to April, 2020, to collect eggs of *R. pedestris* and record the numbers of nymphs and adults. Eggs were brought to the laboratory, individually placed in microtubes (2 mL capacity), and kept in the laboratory. The numbers of newly hatched *R. pedestris* and parasitoids were recorded daily. Additionally, the sex of the newly emerged parasitoids was recorded. Eggs that produced neither a host nymph nor an adult parasitoid were dissected under a stereomicroscope. Host eggs containing parasitoids that failed to develop or emerge were considered parasitized. Each sampling plot was spaced 200 meters apart at each location.

Table 1. Study site and coordinates for the present study.

Site number	Location	Coordinates
Site 1	Kornai	25°42'9.172N, 88°38'26.449E
Site 2	Shadipur	25°42'46.08N, 88°39'45.036E
Site 3	HSTU Campus	25°41'50.748N, 88°39'9.792E

Table 2. Specimens of *H. pubescens* and a closely related specimen with COI barcodes.

Species	CUID	GenBank Accession	Locality
Hadronotus pubescens	FSCA 00094687	MZ513578	Taiwan
Hadronotus pubescens	FSCA 00094882	MZ147017	Bangladesh
Hadronotus pubescens	FSCA 00094879	MZ147018	Bangladesh
Hadronotus sp.	SAM-HYM-P093638	MZ513595	South Africa

Monitoring of *R. pedestris* and its egg parasitoids by pheromone traps

Aggregation pheromone traps were made locally with an iron frame covered with mosquito netting (32 L × 13 D cm). Each trap had two separate openings that enabled entry of *R. pedestris*. Inside the traps were aggregation pheromone lures (Green Agro-Tech Co. Ltd., Kyungsan, Republic of Korea, 50 µL/lure). [Myristyl isobutyrate, (*E*)-2-hexenyl (*E*)-2-hexenoate and (*E*)-2-hexenyl (*Z*)-3-hexenoate at the ratio 1:5:1], and the traps were suspended in the mung bean canopy from a cord attached to the end of a bamboo pole. Inside the trap, a cord was affixed to provide a substrate for egg laying by *R. pedestris* adults. Three pheromone traps were installed at each location (Table 1). Adults and nymphs of *R. pedestris* were recorded at 10-day intervals and the eggs laid by adult *R. pedestris* were collected, brought into the laboratory, placed in micro tubes individually and kept at ambient temperature. The hatching of host insects and the emergence of adult parasitoids were recorded daily.

Effects of host egg age on host acceptance behavior by *H. pubescens*

After 0, 24, 48, 72 and 96 hours from the time that the eggs were laid, eggs were placed in an insect breeding Petri dish (4 H × 10 D cm) at room temperature. Then, a single, mated and naive, 4-day old female *H. pubescens* was introduced into each Petri dish. Host acceptance behaviors were observed under a stereomicroscope (AmScope SM-2TZ LWD, USA) and categorized as drumming, drilling, marking, and oviposition (Strand and Vinson 1983; Noda 1993). The time spent performing each behavior was recorded for each of the eggs when the parasitoid displayed complete host acceptance behavior. The entire procedure was repeated with 10 female parasitoids at each time interval.

Effect of host eggs age on the biological parameters of *H. pubescens*

After 0, 24, 48, 72 and 96 hours from the time that the eggs were laid, 10 eggs of *R. pedestris* were placed on an insect breeding dish (4 H × 10 D cm), and a 4-day old, mated *H. pubescens* female was allowed to parasitize the eggs for 24 hours at ambient conditions.

After 24 hours the female was withdrawn, and the eggs were then placed individually in 2 mL micro tubes with a drop of honey. The eggs were checked daily for the emergence of parasitoids. The number of host eggs parasitized, adult emergence, sex ratio, development time and longevity of male and female *H. pubescens* were recorded. Host eggs containing parasitoids that failed to develop or emerge were also considered parasitized, as determined by dissection of each egg. These procedures were replicated 10 times for each age period.

Each parasitoid that emerged was collected and placed in a 50 mL rearing tube. To maximize longevity, fresh honey and moistened cotton were provided every three days, and the parasitoids were transferred to new tubes as needed. To determine the effect of time on the size of the emerged parasitoids, a total of 30 individuals, both males and females, were randomly selected in each group and their hind tibia lengths were measured under a stereomicroscope (Am Scope, China.) using a micrometer.

Statistical analyses

Emergence rate, adult sex ratio and seasonal parasitism rate were subjected to a chi-square test of a contingency table and a Tukey-type multiple comparison test for post hoc analysis (Zar 2010). The number of parasitized host eggs, number of emerged parasitoids, development time, and hind tibia length of parasitoids was analyzed by a Kruskal-Wallis single factor analysis of variance by rank. If significance was detected, multiple comparisons were conducted using the Duncan test (Zar 2010). The number of eggs, nymphs and adults recorded in the field were analyzed by a univariate analysis of variance by rank. If significance was detected, multiple comparisons were conducted using the Duncan test (Zar 2010). Statistical analyses were performed in IBM SPSS Statistics for Windows.

Results

Taxonomy

Hadronotus pubescens (Motcshoulsky)
Figs 1–11

Muscidea pubescens Motschoulsky, 1863: 70 (original description).
Gryon pubescens (Motschoulsky): Masner 1976: 57 (generic transfer, type information); Johnson 1992: 395 (cataloged, type information).
Gryon hogenakalensis Sharma, 1982: 329, 336 (original description, keyed); Lê, 1997: 23 (keyed); Lê, 2000: 99, 118 (description, keyed, type information).
Gryon hogenakalense Sharma: Johnson 1992: 384 (cataloged).
Hadronotus pubescens (Motchoulsky): Talamas et al. 2021: 441 (generic transfer).
Hadronotus hogenakalensis (Sharma) syn. nov.: Talamas et al. 2021: 423 (generic transfer).

Images of holotype specimens. *Muscidea pubescens*: https://zenodo.org/record/4924954#.YkMH-PnMJaQ. *Gryon hogenakalensis*: USNMENT01197123.

Description. Color of body: dark brown to black. Color of antenna in female: radicle black, A1–A6 yellow-brown with scape darker in middle, A7–A12 black. Color of legs: coxae and femora brown; trochanters, tibiae and tarsi yellow to pale brown. Body length of female: 1.07–1.43 mm (n = 12). Body length of male: 1.34–1.38 mm (n = 2).

Head: Claval formula: A12–A7: 1-2-2-2-2. Number of mandibular teeth: 3. Size of mandibular teeth: small, middle tooth the smallest. Shape of clypeus: transverse, not projecting ventrally, apex flat. Number of clypeal setae: 6, lateral pair very short; medial pairs approximately equal in length; Epiclypeal carina: present. Facial striae: absent. Central keel: present in lower portion of frons. Line of setae above interantennal process: absent. Sculpture of ventral frons: strigose, strigae arching slightly ventrally from central keel, sometimes extending to inner orbit. Sculpture of dorsal frons: transversely strigose medially, weakly rugulose along inner orbit of compound eye. Preocellar pit: absent. Malar striae: absent. Sculpture of gena directly above mandibles: smooth. Genal carina: absent. Occipital carina: continuous medially, with sharp corner behind dorsal apex of compound eye. Anterior margin of occipital carina on gena: crenulate. Anterior margin of occipital carina on posterior head: simple. Hyperoccipital carina: present. Marginal carina: present. Sculpture of occiput: arched, parallel rugae.

Mesosoma: Epomial carina: present. Sculpture of pronotum posterior to epomial carina: transversely rugose. Sculpture of pronotum anterior to epomial carina: smooth. Sculpture of pronotum dorsal to epomial carina: pustulate-punctate. Netrion sulcus: absent. Pronotal suprahumeral sulcus: absent. Setation of lateral pronotum: white; uniformly dense dorsal topomial carina, with small setal patch directly anterior to epomial carina. Mesoscutal suprahumeral sulcus: absent. Mesoscutal humeral sulcus: indicated by a shallow smooth furrow. Mesoscutal humeral pit: present. Sculpture of mesoscutum: reticulate-punctate, with longitudinal rugae in posteromedial portion. Setation of mesoscutum: white, mostly uniform in density, slightly sparser lateral to parapsidal line. Scutoscutellar sulcus: smooth furrow medially, striate laterally. Sculpture of mesoscutellar disc: longitudinally rugose medially, with coarse microsculpture throughout. Posterior mesoscutellar sulcus: foveate.

Posterior margin of mesoscutellum: not extending over metanotum, metascutellum visible in dorsal view. Posterior margin of metascutellum: convex. Sculpture on posteroventral surface of metascutellum: finely strigose. Sculpture of metanotal trough: foveate. Lateral propodeal area: narrow, deeply foveate with white setation. Lateral propodeal carina: extending laterally to metapleural carina, forming flange around metasomal depression. Sculpture of metasomal depression: radially rugulose. Sulcus of the propodeal foramen: foveate.

Postacetabular sulcus: crenulate. Posterior limit of acetabulum: intersecting with ventral mesopleural carina. Mesopleural epicoxal sulcus: composed of shallow foveae. Episternal foveae: absent. Mesopleural carina: present, parallel to acetabular carina. Sculpture of mesopleuron above mesopleural carina: transversely rugose. Femoral depression: not indicated. Prespecular sulcus: composed of large foveae. Sculpture of speculum: transversely rugose. Shape of subalar pit: roughly circular. Mesepimeral
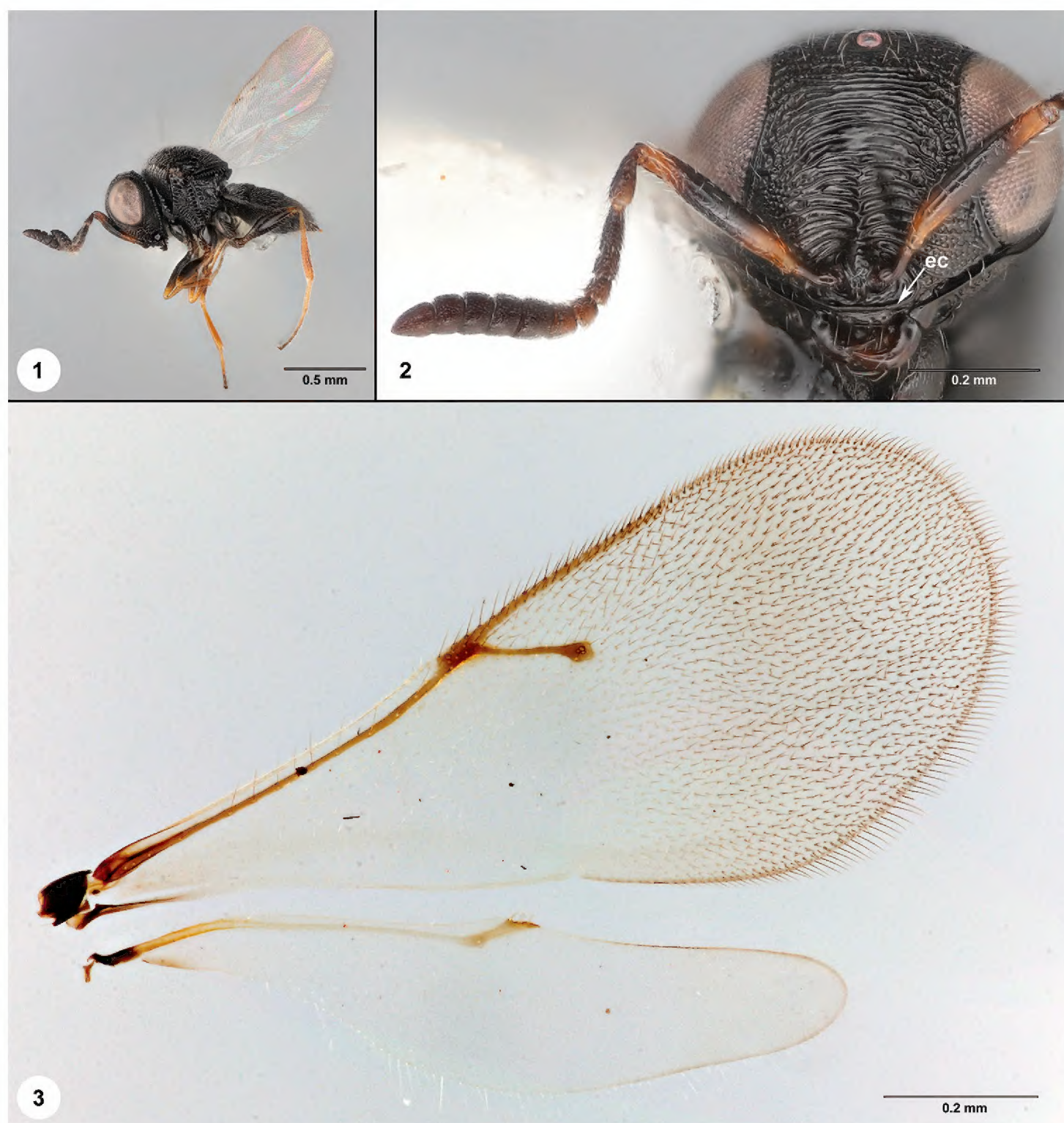
Figures 1–3. *Hadronotus pubescens*, female (FSCA 00094879) **1** lateral habitus **2** head, anterior view **3** wings.

sulcus: foveate, foveae of uniform size. Posterior mesepimeral area: smooth, narrow. Paracoxal sulcus: foveate, absent in ventral part of metapleuron. Metapleural epicoxal sulcus: foveate. Dorsal metapleural area: smooth, with white setation posteriorly. Ventral metapleural area: irregularly rugulose, setose. Posterodorsal metapleuron sulcus: foveate, present along entirely of metapleural carina.

Wings: Length of postmarginal vein in fore wing: almost twice as long as stigmal vein. Length of marginal vein in fore wing: about one third as long as stigmal vein. Color of wing disc: hyaline. Color of fore wing setation: brown in distal half, white in basal half. Color of hind wing setation: white throughout. Shape of submarginal vein: shallowly curved, nearly parallel to wing margin, without sharp bend.
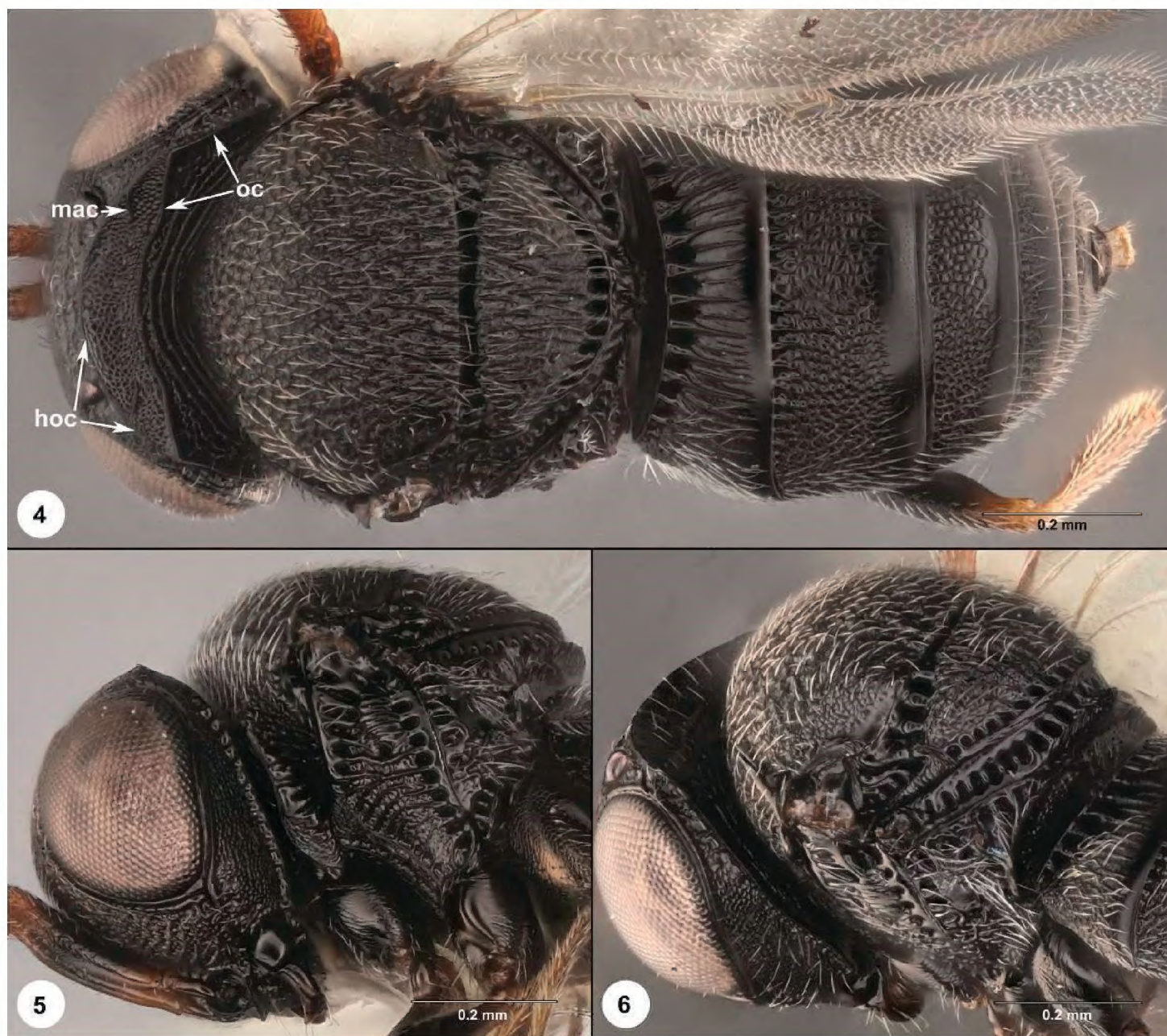
Figures 4–6. *Hadronotus pubescens*, female (FSCA 00094879) **4** head, mesosoma, metasoma, dorsal view **5** head and mesosoma, lateral view **6** head, mesosoma, metasoma, posterolateral view.

Metasoma: Basal foveae: present on T1–T2, S1–S2. Setation of T1–T3: present on lateral portions of tergite. Setation of T2–T5: dense in lateral part of tergite, absent medially except for a transverse line of sparse setae along posterior margin. Sculpture of T1: longitudinally striate, smooth along posterior margin. Sculpture of T2–T4: finely reticulate with a smooth band along posterior margin. Posterior margin of T5: concave. Setation of laterotergites: present. Sculpture of ventral metasoma: reticulate microsculpture throughout. Setation of ventral metasoma: absent from anterolateral S2, otherwise evenly setose throughout.

Intraspecific variation: The specimens examined here are phenotypically uniform, with slight variation occurring in the degree to which transverse striation is developed on the frons and how far the striation extends laterally. The specimens from Bangladesh showed little variation in size, with females ranging from 1.25–1.43 mm. The female specimen from Taiwan was significantly smaller (1.07 mm).
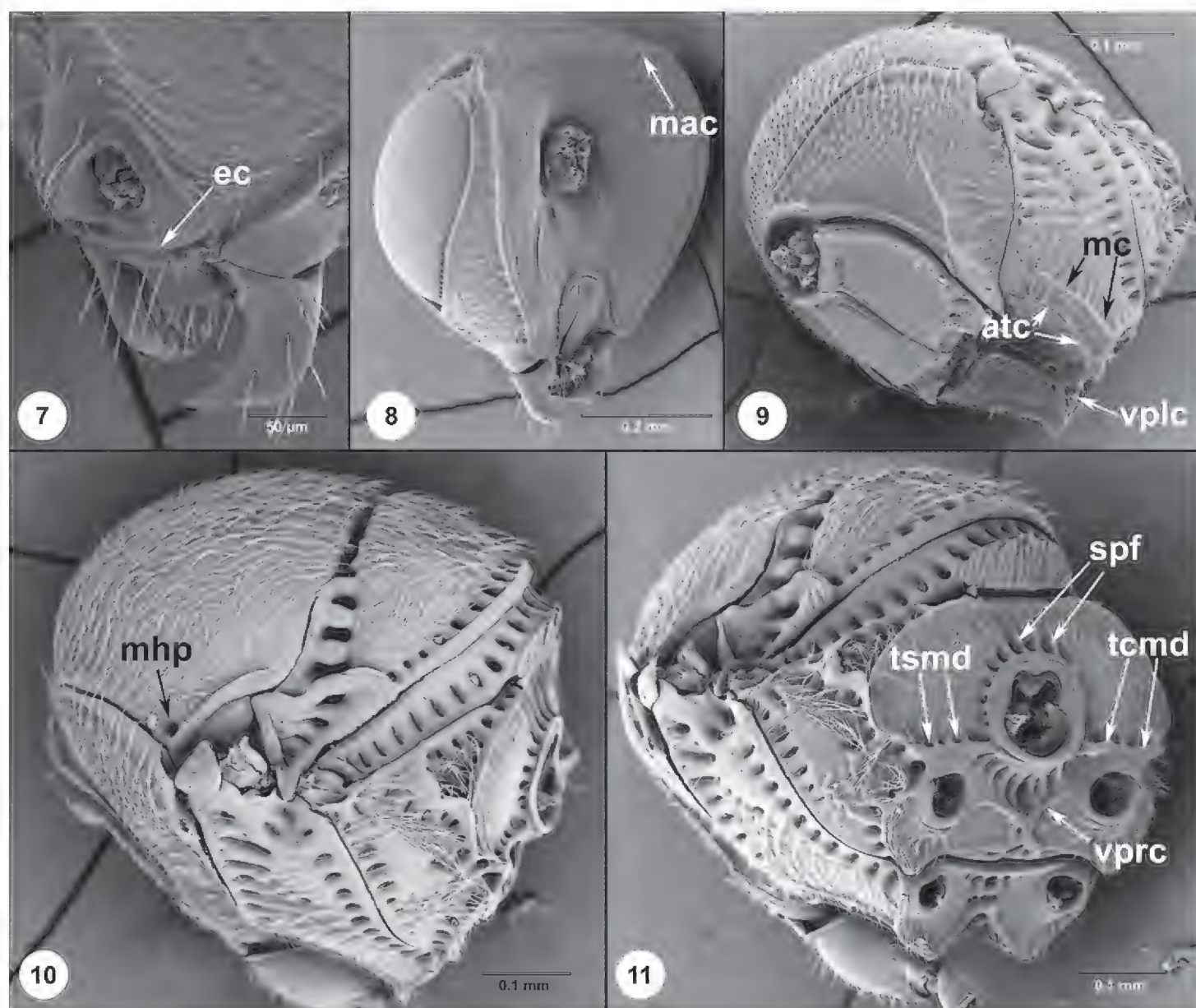
Figures 7–11. *Hadronotus pubescens*, female (FSCA) **7** ventral frons, anterolateral view **8** head, postero-lateral view **9** mesosoma, ventrolateral view **10** mesosoma, dorsolateral view, **11** mesosoma, posterolateral view. Scale bars in millimeters.

Material examined. *Holotype*, female, *Muscidea pubescens* Motchoulsky: **Sri Lanka:** Nuwara Eliya, ZMMU 0001 (ZMMU). Holotype, female, *Gryon hogenakalensis* Sharma: **India:** Hogenakal, 1-FEB-1977, coll. Mani, M. S., USNMENT01137123 (USNM). **Bangladesh:** 12 females, 2 males, DPI_FSCA 00008722, FSCA 00034113–00034118, 00034090–00034094, 00094879, 00094882 (FSCA). **Taiwan:** 1 female, FSCA 00094687 (FSCA).

Comments. *Hadronotus pubescens* is a widespread species, ranging at least from Sri Lanka to Taiwan based on the specimens examined here. The COI sequences from the Taiwanese and Bangladesh specimens share 99.83% sequence identity, providing strong molecular support that they are conspecific. However, a more comprehensive examination of the species limits of *H. pubescens* is still needed and will require analysis of specimens from an even greater geographic range. We examined specimens from South Africa that are morphologically very similar to *H. pubescens* in Asia, pres-

ently separable only by the color of the appendages, yet their COI sequences differ by nearly 13%.

Hadronotus pubescens belongs to a lineage, the *pubescens* species group, that Mineo (1980) defined primarily by the presence of a "marginal carina" (Figs 4, 8, *mac*), which extends medially from the hyperoccipital carina. Two characters provide evidence that this lineage is close to the *charon* species group: the mesoscutal humeral pit (Fig. 10, mhp) and the epiclypeal carina (Figs 2, 7, ec). The mesoscutal humeral pit was first documented by Chen et al. (2020) in *H. ancinla* (Kozlov & Lê) and is present in all species of the *charon* group that we have examined. The antennal scrobe in the *charon* group is entirely delimited by a continuous carina. We consider the ventral, transverse portion of this carina to be homologous with the epiclypeal carina, as is found in *H. pubescens*. The taxon sampling in the multi-gene phylogeny presented in Fig. 2 of Talamas et al. (2021) does not allow for analysis of the monophyly or delimitation of these two species groups. The systematics of *Hadronotus* is ongoing and treatment of species groups within the genus is a research priority.

The metapectal propodeal complex contains morphological characters that have yet to be fully exploited in *Hadronotus*. Carinae and sulci on the metasomal depression vary remarkably among species that we have examined and are likely to become more informative as they are studied in greater detail. The ventral mesopleural carina delimits the posterior margin of the metapleuron on the venter and may be interrupted by the foramen of the hind coxa, as in *H. pubescens* (Figs 9, 11). A transverse carina often extends from the propodeal foramen across the metasomal depression and may be accompanied by a sulcus (Fig. 11). Talamas et al. (2021) provided the term "sulcus of the propodeal foramen" for *Gryon aetherium* Talamas, which is present only dorsally. In *H. pubescens*, foveae are present ventral to the transverse carina on the metasoma depression. It is presently unclear if these foveae are a continuation of the sulcus of the propodeal foramen or an independent structure.

Biological parameters

Abundance of *R. pedestris* and its egg parasitoids in different locations

All life stages of *R. pedestris* were found throughout the sampling period. The occurrence of *R. pedestris* eggs, nymphs, and adults started in February and peaked in the month of April. The seasonal number of eggs ($H_C = 11.201$, $df = 8$, $P = 0.076$), nymphs ($H_C = 11.028$, $df = 8$, $P = 0.284$) and adults ($H_C = 3.00$, $df = 8$, $P = 0.876$) of *R. pedestris* was not significantly different among the three different locations (Fig. 12). The number of both unparasitized and parasitized eggs was higher in the mung bean field in Shadipur compared to the other two locations (Fig. 13). The number of unparasitized eggs ($H_C = 1.192$, $df = 8$, $P = 0.981$) and parasitized eggs ($H_C = 8.998$, $df = 8$, $P = 0.98$) were not significantly different among the three locations (Fig. 13). The total parasitism rate of natural host eggs at each sampling site was separated by parasitoid species, i.e., solitary parasitoid *Hadronotus pubescens* and gregarious parasitoids like *Ooencyrtus* sp. Throughout the sampling period, the total parasitism rate
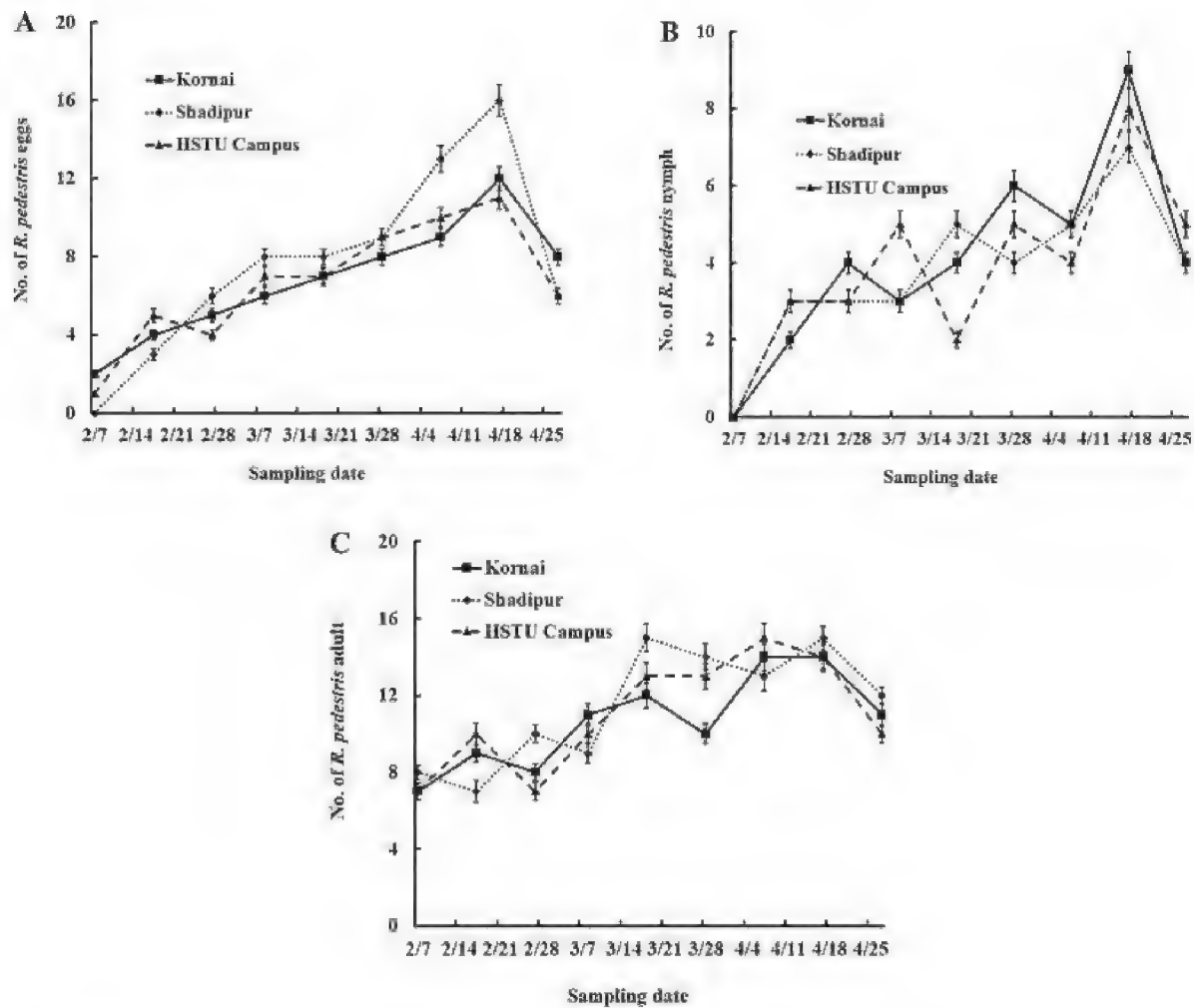
Figure 12. Mean number of eggs (**A**), nymphs (**B**), and adults (**C**) of *R. pedestris* sampled from three different study sites. Analyses were conducted on the seasonal data using Kruskal-Wallis single factor analysis of variance by rank.
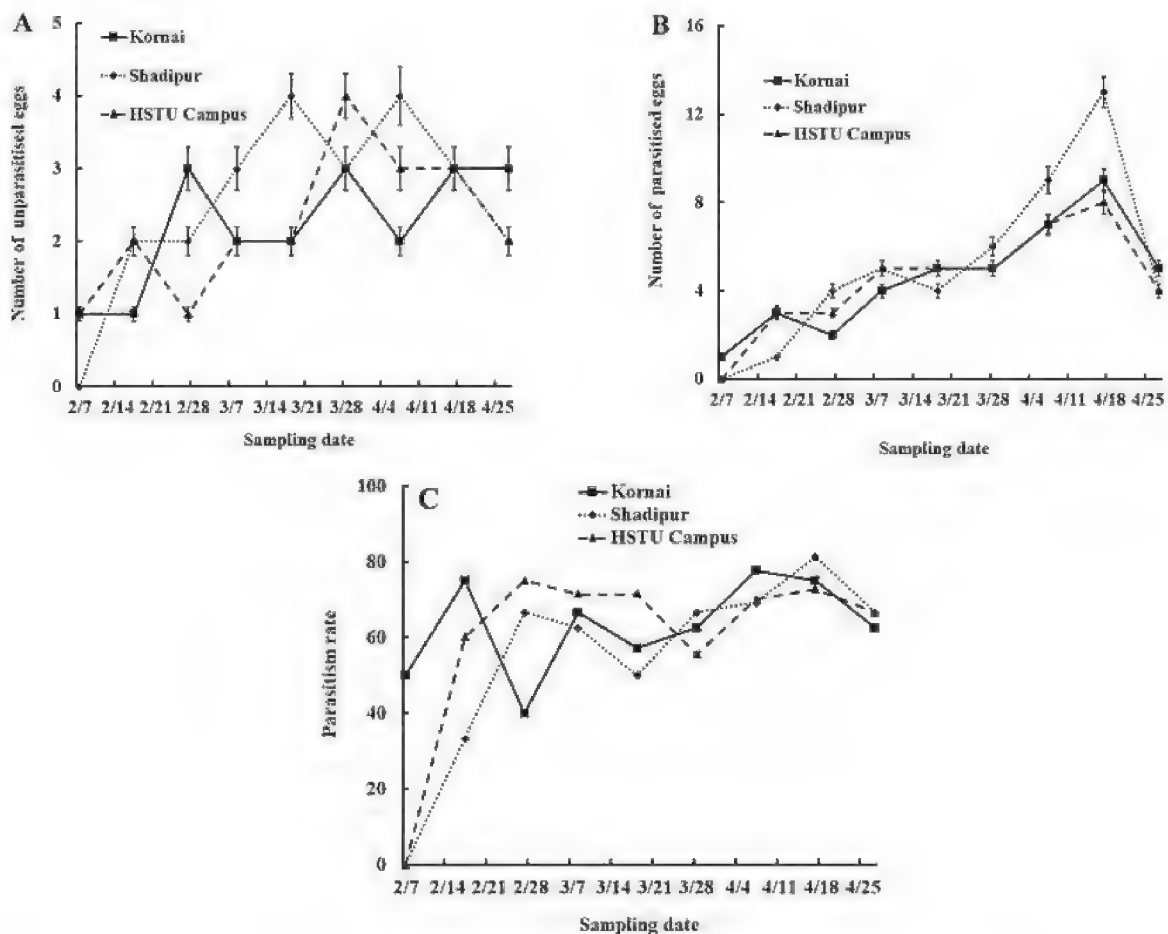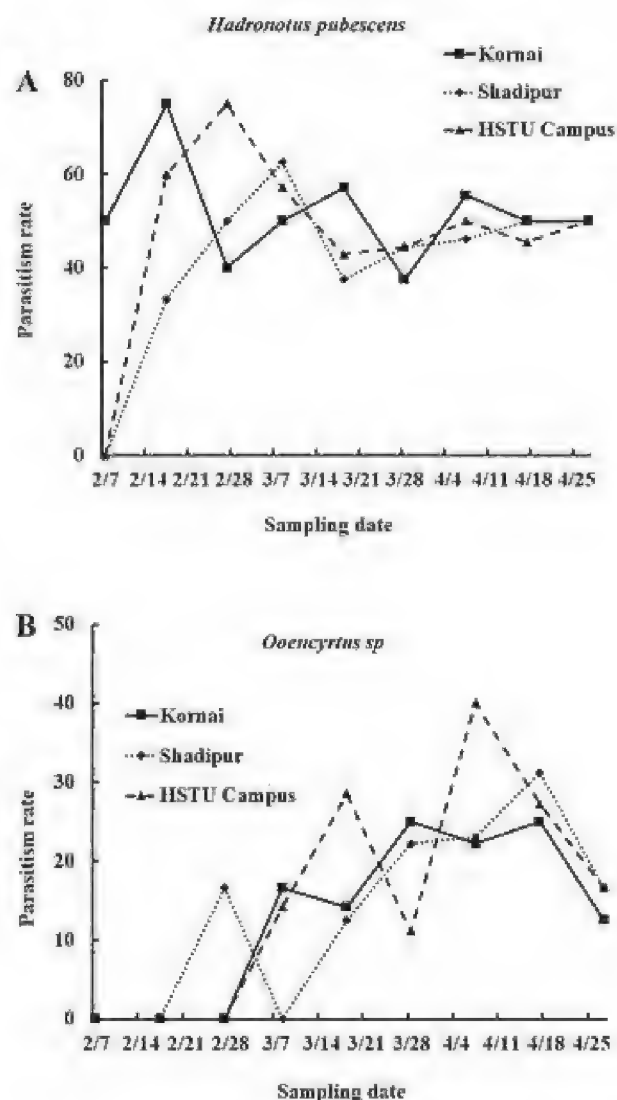

Figure 13. Parasitism rate (%) of natural *R. pedestris* eggs collected from three different study sites. Analyses were conducted on the seasonal data using Kruskal-Wallis single factor analysis of variance by rank.

Figure 14. Parasitism rates by *H. pubescens* (**A**) and *Ooencyrtus* sp. (**B**) on natural eggs collected from three different study sites.

by both species was found to be higher in Kornai compared to HSTU campus and Shadipur mung bean field ($\chi^2 = 0.005$, $df = 2$, $P = 0.997$) (Fig. 13). The total parasitism rates by both parasitoid species were higher in the month of April, when the mung bean seeds were maturing. The parasitism rate by *H. pubescens* on naturally-laid host eggs was higher in Kornai than in Shadipur or the HSTU Campus ($\chi^2 = 5.371$, $df = 8$, $P = 0.639$) (Fig. 14). On the other hand, the parasitism rate of *Ooencyrtus* sp.alone ($\chi^2 = 9.746$, $df = 8$, $P = 0.201$) was highest in the HSTU campus among the three study sites (Fig. 14).

Monitoring of *R. pedestris* and its egg parasitoids by pheromone traps

Throughout the sampling period, the number of eggs, nymphs, and adults of *R. pedestris* found in the pheromone traps differed between the sites. The seasonal numbers of eggs ($H_C = 7.513$, $df = 8$, $P = 0.341$), nymphs ($H_C = 10.096$, $df = 8$, $P = 0.268$), and adults ($Hc = 14.415$, $df = 8$, $P = 0.254$) of *R. pedestris* were not significantly different among the study sites (Fig. 15). However, the numbers of eggs, nymphs, and adults of *R. pedestris* caught by pheromone traps was higher on the HSTU campus than at the other two sites in the month of April. The number of unparasitized eggs was higher
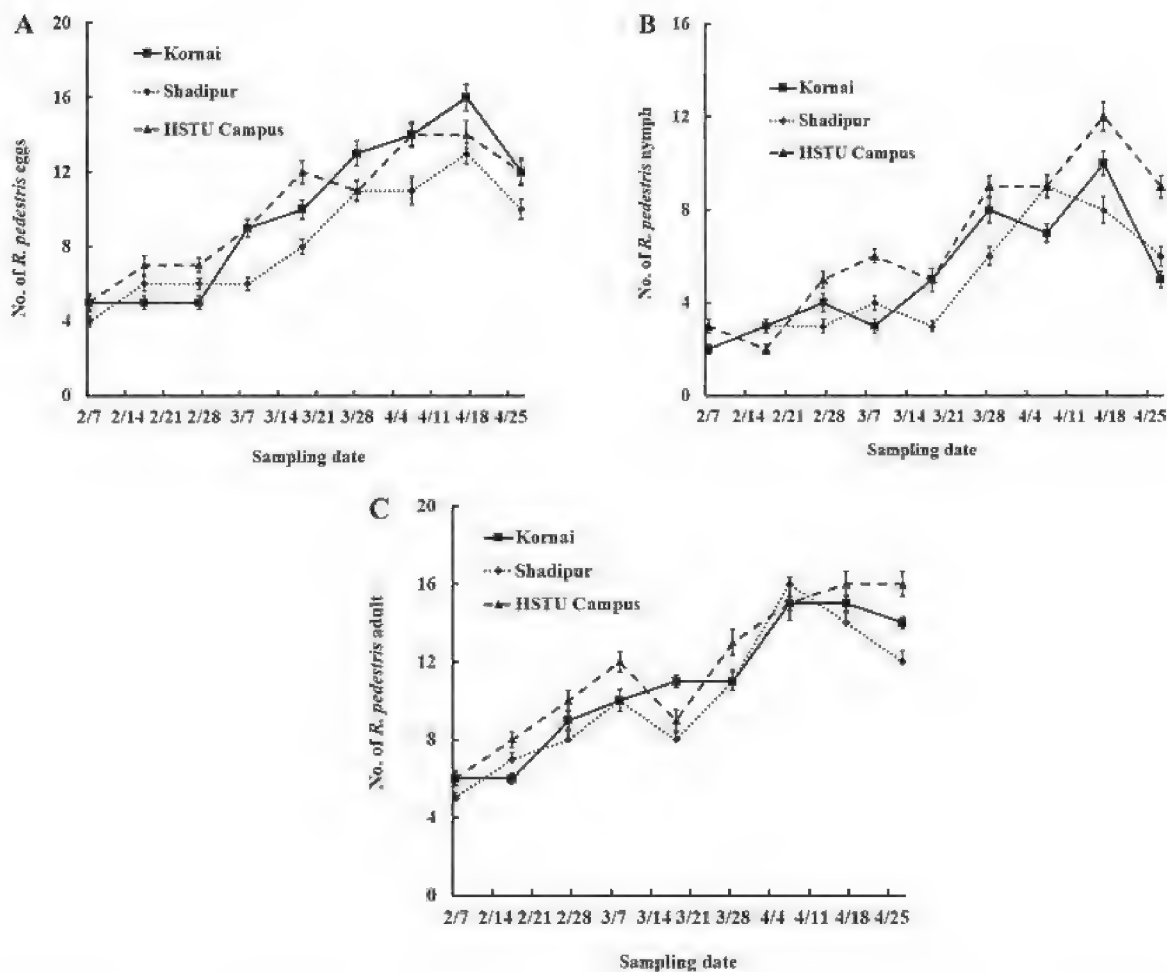
Figure 15. Mean number of eggs (**A**), nymphs (**B**), and adults (**C**) of *R. pedestris* collected from aggregation pheromone traps from three different study sites. Analyses were conducted on the seasonal data using Kruskal-Wallis single factor analysis of variance by rank.

on the HSTU campus compared to the other two sites, and the number of parasitized eggs was higher in Kornai compared to other locations in the month of April. The seasonal numbers of unparasitized eggs (H_C = 0.507, *df* = 8, *P* = 1.00) and parasitized eggs (H_C = 6.302, *df* = 8, *P* = 0.330) were not significantly different among the three different locations (Fig. 16). Throughout the sampling period, the total parasitism rate was not significantly different but was higher in the month of April in Kornai compared to the other sites (χ^2 = 0.862, *df* = 2, *P* = 0.649) (Fig. 16).

The total parasitism rate on natural host eggs at each sampling site was separated by parasitoid species, i.e., *H. pubescens* and *Ooencyrtus* sp. The overall parasitism rate by *H. pubescens* peaked in February and was lowest in April, whereas parasitism by *Ooencyrtus* sp. peaked in April and was lowest in February. The parasitism rate of both *H. pubescens* (χ^2 = 2.440, *df* = 8, *P* = 0.827) and *Ooencyrtus* sp. (χ^2 = 7.745, *df* = 8, *P* = 0.357) were not statistically different among sites and were highest in Kornai (Fig. 17).

Effects of host egg age on host acceptance behavior by *H. pubescens*

All *H. pubescens* showed a complete process of host acceptance behaviors on the eggs of *R. pedestris*. Each phase consisted of one or more bouts. The duration of host acceptance behaviors displayed by the egg parasitoids is shown in Table 3. Drumming was
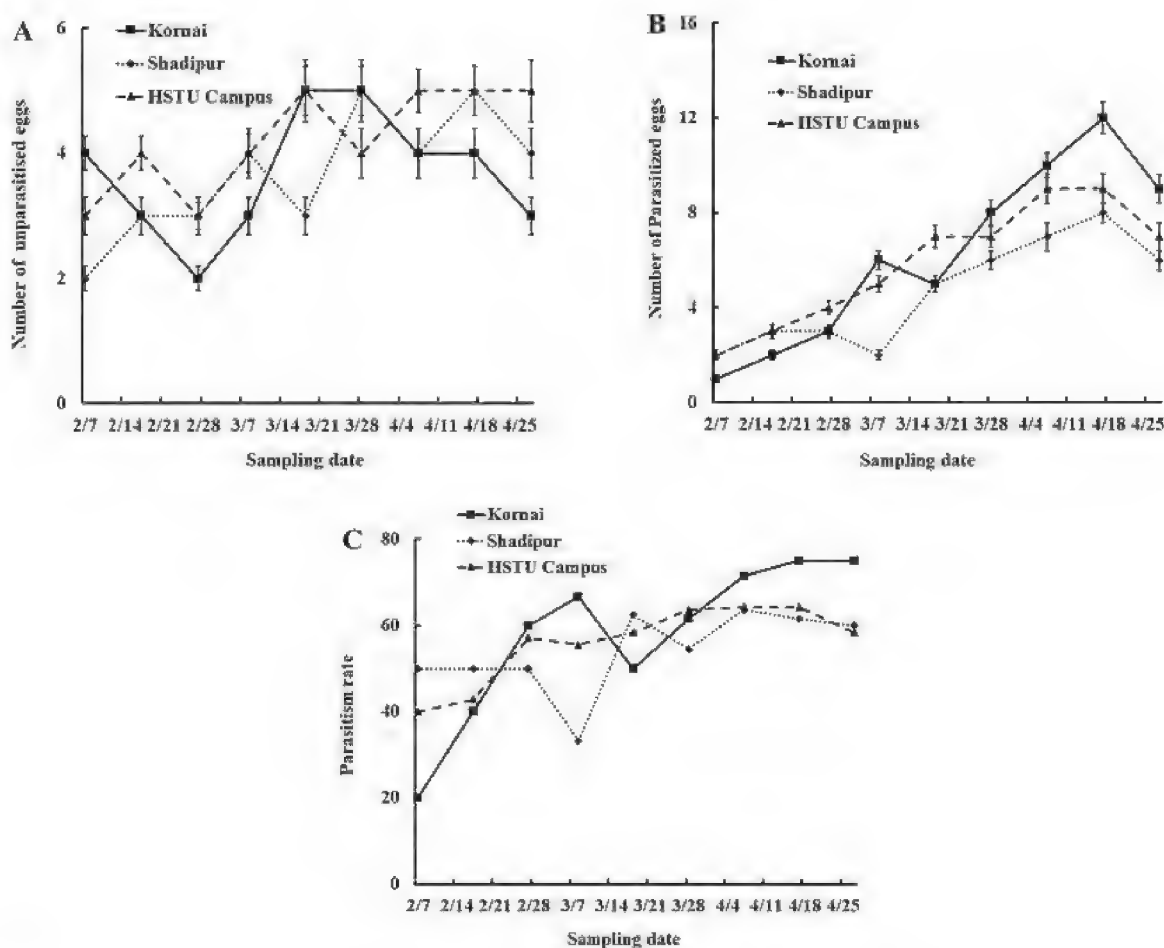
Figure 16. Parasitism rate of natural *R. pedestris* eggs collected from aggregation pheromone traps from three different study sites. Analyses were conducted on the seasonal data using Kruskal-Wallis single factor analysis of variance by rank.

characterized by moving antennae up and down over the exposed surface of the eggs while the female remained still, standing over the eggs. The duration of drumming increased as the age of the host egg increased (H_C = 43.562, *df* = 4, *P* < 0.001) (Table 3). The 96 hr old eggs of *R. pedestris* received the longest duration of drumming by the parasitoid. The female parasitoid started drilling after the drumming by inserting her ovipositor into the host eggs. After head pumping, the female remained motionless for 10–15 seconds until oviposition was completed. The mean time spent on drilling and oviposition increased as the age of the host egg increased. The eggs of *R. pedestris* at 96 hours showed the longest duration of drilling and oviposition by the parasitoid. (H_C = 47.063, df = 4, *P* < 0.001) (Table 3). Similarly, females of *H. pubescens* spent more time marking eggs that were 96 hours old compared to eggs of other ages (H_C = 47.059, df = 4, *P* < 0.001) (Table 3).

Table 3. Duration (seconds ± SE) of host acceptance behaviors in different ages of *R. pedestris* eggs Numbers in each row followed by the same letter are not significantly different (*P* > 0.05).

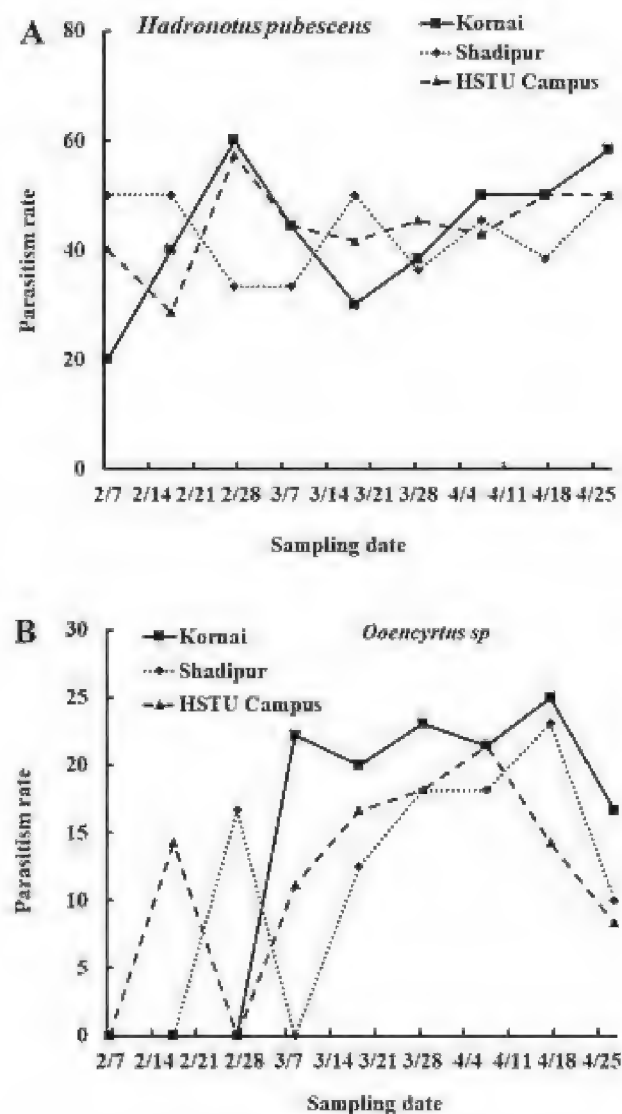| Behaviors	Age of host eggs (hours)				
	0 (Control)	**24**	**48**	**72**	**96**
Drumming	37.58±0.68 d	47.09±0.30 b	40.88±0.67 c	48.89±0.96 b	58.30±0.68 a
Drilling & Oviposition	413.11±0.98 e	490.04±0.88 c	437.53±1.15 d	549.85±1.03 b	588.91±0.77 a
Marking	137.53±1.22 e	148.98±1.11 d	171.67±0.94 c	190.25±0.91 b	210.74±0.72 a

Figure 17. Parasitism rate by *H. pubescens* (**A**) and *Ooencyrtus* sp. (**B**) on natural eggs collected from three different study sites from inside the aggregation pheromone traps.

Effect of host egg age on the biological attributes of *Hadronotus pubescens*

The number of eggs parasitized by *H. pubescens* was influenced by the age of the host eggs. *Hadronotus pubescens* can successfully parasitize host eggs up to 48 hours old without a change in the parasitism rate ($H_C = 10.813$, $df = 4$, $P = 0.029$) (Table 4). However, for the host eggs 96 hours old, the parasitism rate decreased approximately 14% compared to the control (Table 4). The emergence rate ($H_C = 8.802$, $df = 4$, $P = 0.662$) and the sex ratio ($\chi^2 = 6.416$, $df = 4$, $P = 0.170$) of *H. pubescens* were unaffected by host egg ages (Table 4). However, the total number of parasitoids that emerged from parasitized eggs significantly decreased with the increase in the host egg age. The sex ratios of the emerged parasitoids were all female biased. The mean development time (from egg to adult) of *H. pubescens* males and females increased significantly as host egg age increased (male $H_C = 14.288$, $df = 4$, $P < 0.001$; female $H_C = 105.398$, $df = 4$, $P < 0.001$) (Table 4). The highest mean development time for both males and females was found in eggs 96 hours in age and was lowest in the control (0 hours). The longevity of male and female *H. pubescens* decreased significantly when host egg age increased (male $H_C = 41.432$ $df = 4$ $P < 0.001$; female $H_C = 192.442$ $df = 4$ $P < 0.001$) (Table 4). The highest longevity was found at 0 hours of age (control) compared to the other treatments.

Table 4. Biological attributes of *H. pubescens* on different age of *R. pedestris* eggs. Numbers in each row followed by the same letter are not significantly different (*P* > 0.05).

	Age of host eggs (hours)				
	0	**24**	**48**	**72**	**96**
Number parasitized host eggs /female ± SE	9.10 ± 0.27 a	8.60 ± 0.52 ab	8.40 ± 0.26 ab	8.30 ± 0.36 ab	7.70 ± 0.15 b
Proportion of male	0.13 (12/91)	0.10 (9/86)	0.21 (18/84)	0.14 (12/83)	0.10 (9/86)
Emergence rate	0.90 (90/100)	0.83 (83/100)	0.82 (82/100)	0.82 (82/100)	0.74 (74/100)
Development time, day ± SE					
Male	14.75±0.16 b	14.88±0.14 b	15.12±0.12 ab	15.22±0.10 ab	15.58±0.14 a
Female	14.88±0.06 c	14.91±0.06 c	15.41±0.08 b	15.19±0.04 b	15.72±0.05 a
Longevity, day ± SE					
Male	23.16±0.18 a	22.42±0.20 a	20.75±0.81 a	15.25±0.45 b	15.50±0.86 b
Female	25.12±0.10 a	24.50±0.18 a	24.27±0.30 a	20.61±0.44 b	17.60±0.41 c

Discussion

Throughout the sampling period, eggs, nymphs, and adults of *R. pedestris* were found in the three mung bean fields that we sampled. All life stages of *R. pedestris* were observed early in the mung bean season (February) and increased in abundance in April. Son et al. (2008) reported *R. pedestris* in different fruit orchards starting in the last week of April and found the highest abundance in June and October. *Riptortus pedestris* populations were found to start infesting soybeans in the second week of August, with a population peak occurring in the first half of September (Kim and Lim 2010). In the present study, nymphs were caught in pheromone traps during the whole experimental period at the three different locations. The highest number of nymphs was attracted by pheromone traps in the month of April. The synthetic pheromone was effective in attracting second instar *R. pedestris* nymphs only. Leal et al. (1995) speculated that older nymphs do not respond because they may not need information to locate a food source as they have already reached the host plant. The *R. pedestris* adults were attracted to pheromone traps starting in the month of February and showed the highest levels of attraction in the middle of April. Adults of *R. pedestris* were found in traps on barley in the second week of April. The population then increased and peaked in the last week of August on soybeans, and sharply decreased in October (Mainali and Lim 2012).

In this study, we confirmed that the solitary egg parasitoid *H. pubescens* appears in mung bean fields from the first week of February to the last week of April. On the other hand, gregarious parasitoids *Ooencyrtus* sp. appear in mung bean fields from the middle of February to the end of April.

The differential pattern of occurrence, i.e., *H. pubescens* during spring and *Ooencyrtus* sp. during summer, is a new finding in mung bean fields in Bangladesh. Differences in the temporal patterns of each parasitoid's occurrence could be the result of adaptation to certain environmental conditions such as temperature or humidity. Patterns observed in our survey demonstrated that *H. pubescens* probably perform better in the spring and early summer, when humidity is low, compared to *Ooencyrtus* sp., whose abundance was greatest in the summer when higher humidity was recorded

in Bangladesh. The effects of weather conditions on the timing of occurrence and on biological attributes have been reported for other parasitoid species (Ouedraogo et al. 1996; Rousse et al. 2009; Sorribas et al. 2010).

Another factor that could affect the abundance of adult populations is interspecific competition inside the host eggs. Takasu et al. (1998) found that interactions between adults of *Ooencyrtus* sp. and *Hadronotus* spp. did not influence the reproduction of either species (Takasu et al. 1998). Given that some species of *Ooencyrtus*, eg., *O. nezarae*, are facultative hyperparasitoids, use of these species as biological control agents may reduce the population of other parasitoids in the system, such as *H. pubescens*.

The emergence rate and the sex ratio of *H. pubescens* were unaffected by host egg ages. This, in combination with the increased time spent on host assessment and the lower parasitism rate associated with older eggs, suggests that females of *H. pubescens* discriminate and reject eggs that are too old to be viable for their progeny. The sex ratios of the emerged parasitoids were all female-biased without statistical significance among the different periods. The highest mean development time (male and female) was found at 96 hours of age and the lowest in control (0 hours), which might be due to the lower nutritional quality attributed to older host eggs that can slow the offspring development rate (Godfray 1994). Male and female *H. pubescens* had shorter lifespans as age of the the host eggs increased, perhaps due to reduced nutritional quality of the eggs (Alim and Lim 2009).

Conclusion

This study provides baseline data on the parasitism of *R. pedestris* eggs by *H. pubescens* and a species of *Ooencyrtus* and indicates that *H. pubescens* has potential as a biological control agent. It also showcases the necessity of integrating taxonomy with field studies so that the biological parameters of a species can be confidently associated with a species name. In the case of *H. pubescens*, the species-level treatment provided here is the first since its original description in 1863 and was facilitated by the holotype images and molecular data provided in Talamas et al. (2021). We hope that this paradigm of integration will continue to be employed as additional studies on parasitoids of hemipteran eggs are conducted.

Acknowledgements

References

Alim MA, Lim UT (2011) Refrigerated eggs of *Riptortus clavatus* (Hemiptera: Alydidae) added to aggregation pheromone traps increase field parasitism in soybean. Journal of Economic Entomology 104: 1833–1893. https://doi.org/10.1603/EC11143

Alim MA, Lim UT (2009) Refrigeration of *Riptortus clavatus* (Hemiptera: Alydidae) eggs for the parasitization by *Gryon japonicum* (Hymenoptera: Scelionidae). Biocontrol Science and Technology 19: 315–325. https://doi.org/10.1080/09583150902752020

Arifunnahar M, Ahmed MBU, Hossain MA, Alim MA (2019) Varietal susceptibility of mungbean to pod borer (*Maruca vitrata*), bean bug (*Riptortus pedestris*) and epilachna beetle (*Epilachna decastigma*). Bangladesh Journal of Entomology 29: 49–58.

Arifunnahar M, Khatun MM, Hossain MA, Alim MA (2021) Toxicity evaluation of different chemical pesticides against *Riptortus pedestris* (Hemiptera: Alydidae) under laboratory condition in Bangladesh. Journal of the Bangladesh Agricultural University 19: 192–197. https://doi.org/10.5455/JBAU.72976

Chen H, Talamas EJ, Bon M-C, Moore MR (2020) *Gryon ancinla* Kozlov & Lê (Hymenoptera: Scelionidae): host association, expanded distribution, redescription and a new synonymy. Biodiversity Data Journal 8: e47687. https://doi.org/10.3897/BDJ.8.e47687

Choi MY, Lee GH, Paik CH (2005) Feeding preference, nymphal development time, body-weight increase, and survival rate of the bean bug, *Riptortus clavatus* (Thunberg) (Hemiptera: Alydidae), on soybean varieties. Korean Journal of Applied Entomology 44: 287–292.

Chung BK, Kang SW, Kwon JH (1995) Damages, occurrences and control of hemipterous insects in non-astringent persimmon orchards. Journal of Agricultural Science 37: 376–382.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Giantsis IA, Chaskopoulou A, Bon MC (2016) Mild-Vectolysis: A nondestructive DNA extraction method for vouchering sand flies and mosquitoes. Journal of Medical Entomology 53: 692–695. https://doi.org/10.1093/jme/tjv236

Higuchgi H, Suzuki Y (1996) Host handling behavior of the egg parasitoid *Telenomus triptus* to the egg mass of the stink bug *Piezodorus hybneri*. Entomologia Experimentalis et Applicata 80: 475–479. https://doi.org/10.1111/j.1570-7458.1996.tb00962.x

Hirose Y, Takasu K, Takagi M (1996) Egg parasitoids of phytophagous bugs in soybean: Mobile natural enemies as naturally occurring biological control agents of mobile pests. Biological control 7: 84–94. https://doi.org/10.1006/bcon.1996.0069

Honda K (1986) Estimation of the number of damaged soybean seeds caused by the bean bug, *Riptortus clavatus* Thunberg. Tohoku Agricultural Research 39: 157–158.

Johnson NF (1992) Catalog of world Proctotrupoidea excluding Platygastridae. Memoirs of the American Entomological Institute 51: 1–825.

Kang CH, Huh HS, Park CG (2003) Review on true bugs infesting tree fruits, upland crops, and weed in Korea. Korean Journal of Applied Entomology 42: 269–277.

Kim S, Lim UT (2010) Seasonal occurrence pattern and within-plant egg distribution of bean bug, *Riptortus pedestris* (Fabricius) (Hemiptera: Alydidae), and its egg parasitoids in soy-

bean fields. Applied Entomology and Zoology 45: 457–464. https://doi.org/10.1303/aez.2010.457

Kimura S, Tokumaru S, Kikuchi A (2008) Carrying and transmission of *Eremothecium coryli* (Peglion) Kurtzman as a causal pathogen of yeast- spot disease in soybeans by *Riptortus clavatus* (Thungberg), *Nezara antennata* (Scott), *Piezodorus hyberni* (Gmelin) and *Dolycoris baccarum* (Linnaeus). Japanese Journal of Applied Entomology and Zoology 52: 13–18. https://doi.org/10.1303/jjaez.2008.13

Lahey Z, Talamas E, Masner L, Johnson NF (2021) Revision of the Australian genus *Alfredella* Masner & Huggert (Hymenoptera, Platygastridae, Sceliotrachelinae). In: Lahey Z, Talamas E (Eds) Advances in the Systematics of Platygastroidea III. Journal of Hymenoptera Research 87: 81–113. https://doi.org/10.3897/jhr.87.58368

Lê XH (1997) Ong ky sinh ho Scelionidae (Hymenoptera) ky sinh trong trung bo xit (Heteroptera) o Viet Name. Tap Chi Sinh Hoc 19: 23–28.

Lê XH (2000) Egg-parasites of family Scelionidae (Hymenoptera). Fauna of Vietnam, vol. 3. Science and Technics Publishing House. Hanoi, 386 pp.

Leal WS, Higuchi H, Mizutani N, Nakamori H, Kadosawa T, Ono M (1995) Multifunctional communication in *Riptortus clavatus* (Heteroptera: Alydidae): conspecific nymphs and egg parasitoid *Ooencyrtus nezarae* use the same adult attractant pheromone as chemical cue. Journal of Chemical Ecology 21: 973–985. https://doi.org/10.1007/BF02033802

Lee GH, Paik CH, Choi MY, Oh TJ, Kim DH, Na SY (2004) Seasonal occurrence, soybean damage and control efficacy of bean bug, *Riptortus clavatus* Thunberg (Hemiptera: Alydidae) at soybean field in Honam Province. Korean Journal of Applied Entomology 43: 249–255.

Li K, Zhang XX, Guo JQ, Hannah P, Wu TT, Li L, Jiang H, Chang LD, Wu CX, Han TF (2019) Feeding of *Riptortus pedestris* on soybean plants, the primary cause of soybean staygreen syndrome in the Huang-Huai-Hai river basin. The Crop Journal 7: 360–367. https://doi.org/10.1016/j.cj.2018.07.008

Mainali BP, Kimand HJ, Bae SD (2014) Infestation of *Riptortus pedestris* Fabricius decreases the nutritional quality and germination potential of soybean seeds. Journal of Asia-Pacific Entomology 17: 477–481. https://doi.org/10.1016/j.aspen.2014.04.006

Mainali BP, Lim UT (2012) Annual pattern of occurrence of *Riptortus pedestris* (Hemiptera: Alydidae) and its egg parasitoids *Ooencyrtus nezarae* Ishii and *Gryon japonicum* (Ashmead) in Andong, Korea. Crop Protection 36: 37–42. https://doi.org/10.1016/j.cropro.2012.01.016

Masner L (1976) Revisionary notes and keys to world genera of Scelionidae (Hymenoptera: Proctotrupoidea). Memoirs of the Entomological Society of Canada 97: 1–87. https://doi.org/10.4039/entm10897fv

Mikó I, Vilhelmsen L, Johnson NF, Masner L, Pénzes Z (2007) Skeletomusculature of Scelionidae (Hymenoptera: Platygastroidea): head and mesosoma. Zootaxa 1571: 1–78. https://doi.org/10.11646/zootaxa.1571.1.1

Mineo G (1980) Studies on the Scelionidae (Hym. Proctotrupoidea). XI. A revision of the Palearctic species of *Gryon* Haliday: the *insulare* and *pubescens* groups. Bollettino dell'Istituto di Entomologia Agraria e dell'Osservatorio di Fitopatologia di Palermo 10: 213–226.

Mizutani N, Hirose Y, Higuchi H, Wada T (1996) Seasonal abundance of *Ooencyrtus nezarae* Ishii (Hymenoptera: Encyrtidae), an egg parasitoid of phytophagous bugs, in summer soybean fields. Japanese Journal of Applied Entomology and Zoology 40: 199–204. https://doi.org/10.1303/jjaez.40.199

Motschoulsky VI (1863) Essai d'un catalogue des insectes de l'ile Ceylan. Bulletin de la Société Imperiale des Naturalistes de Moscou. 36(2): 1–153.

Noda T (1989) Seasonal occurrence of egg parasitoids of *Riptortus clavatus* (Thungberg) (Heteroptera: Alydidae) on several leguminous plants. Japanese Journal of Applied Entomology and Zoology 4: 257–259. https://doi.org/10.1303/jjaez.33.257

Noda T (1993) Ovipositional strategy of *Gryon japonicum* (Hymenoptera: Scelionidae). Bulletin of the National Institute of Agro-Environmental Sciences 9: 1–51.

Osakabe M, Honda K (2002) Influence of trap and barrier crops on occurrence of and damage by stink bugs and lepidopterous pod borers in soybean fields. Japanese Journal of Applied Entomology and Zoology 46: 233–241. https://doi.org/10.1303/jjaez.2002.233

Orr DB (1998) Scelionid wasps as biological control agents: A review. Florida Entomologist 71: 506–527. https://doi.org/10.2307/3495011

Ouedraogo PA, Sou S, Sanon A, Monge JP, Huignard J, Tran B, Credland PF (1996) Influence of temperature and humidity on populations of *Callosobruchus maculates* (Coleoptera: Bruchidae) and its parasitoid *Dinarmus basalis* (Pteromalidae) in two climatic zones of Burkina Faso. Bulletin of Entomological Research 86: 695–702. https://doi.org/10.1017/S0007485300039213

Rabb RL, Bradley JR (1970) Marking host eggs by *Telenomus sphingis*. Annals of the Entomological Society of America 63: 209–215. https://doi.org/10.1093/aesa/63.4.1053

Rousse P, Gourdon F, Roubaud M, Chiroleu F, Quilici S (2009) Biotic and abiotic factors affecting the flight activity of *Fopius arisanus*, an egg-pupal parasitoid of fruit fly pests. Environmental Entomology 38: 896–903. https://doi.org/10.1603/022.038.0344

Schwab AI, Jager I, Stoll G, Gorgen R, Schwab SP, Altenburger R (1995) Pesticides in Tropical Agriculture: Hazards and alternatives. PAN, ACTA, Tropical Agro Ecology, 131 pp.

Sharma SK (1982) On some Scelionidae (Proctotrupoidea: Hymenoptera) from India. Records of the Zoological Survey of India 79: 319–342. https://doi.org/10.26515/rzsi/v79/i3-4/1981/161730

Son C, Park SG, Hwang YH, Choi B (2000) Field occurrence of stink bug and its damage in soybean. Korean Journal of Crop Science 45: 405–410.

Son JK, Nguyen XD, Park CG (2008) Seasonal parasitism of *Riptortus clavatus* Thunberg (Heteroptera: Alydidae) Thunberg by *Dionaea magnifrons* (Herting) (Diptera:Tachinidae). Journal of Asia-Pacific Entomology 11: 191–194. https://doi.org/10.1016/j.aspen.2008.08.001

Son JK, Choo HY, Choi JY, Paik CH, Park CG (2009) Enhancement of *Riptortus clavatus* (Thungberg) (Hemiptera: Alydidae) egg parasitism by a component of the bugs aggregation pheromone. Journal of Asia-Pacific Entomology 12: 159–163. https://doi.org/10.1016/j.aspen.2009.02.009

Sorribas J, Rodriguez R, Garcia-Mari F (2010) Parasitoid competitive displacement and coexistence in citrus agroecosystems: linking species distribution with climate. Ecological Applications 20: 1101–1113. https://doi.org/10.1890/09-1662.1

Strand MR, Vinson SB (1983) Host acceptance behavior of *Telenomus heliothidis* (Hymenoptera: Scelionidae) toward *Heliothis virescens* (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 76: 781–785. https://doi.org/10.1093/aesa/76.4.781

Takasu K, Hirose Y, Takagi M (1998) Occasional interspecific competition and within plant microhabitat preference in egg parasitoids of the bean bug, *Riptortus clavatus* (Hemiptera: Alydidae) in soybean. Applied Entomology and Zoology 33: 391–399. https://doi.org/10.1303/aez.33.391

Talamas EJ, Thompson J, Cutler A, Fitzsimmons Schoenberger S, Cuminale A, Jung T, Johnson NF, Valerio AA, Smith AB, Haltermann V, Alvarez E, Schwantes C, Blewer C, Bodenreider C, Salzberg A, Luo P, Meislin D, Buffington ML (2017) An online photographic catalog of primary types of Platygastroidea (Hymenoptera) in the National Museum of Natural History, Smithsonian Institution. In: Talamas EJ, Buffington ML (Eds) Advances in the Systematics of Platygastroidea. Journal of Hymenoptera Research 56: 187–224. https://doi.org/10.3897/jhr.56.10774

Talamas EJ, Bremer JS, Moore MR, Bon M-C, Lahey Z, Roberts CG, Combee LA, McGathey N, van Noort S, Timokhov AV, Hougardy E, Hogg B (2021) A maximalist approach to the systematics of a biological control agent:*Gryon aetherium* Talamas, sp. nov. (Hymenoptera, Scelionidae). In: Lahey Z, Talamas E (Eds) Advances in the Systematics of Platygastroidea III. Journal of Hymenoptera Research 87: 323–480. https://doi.org/10.3897/jhr.87.72842

Wada T, Endo N, Takahashi M (2006) Reducing seed damage by soybean bugs by growing small-seeded soybeans and delaying sowing time. Crop Protection 25: 726–731. https://doi.org/10.1016/j.cropro.2005.10.003

Weber CA, Smilanick JM, Ehler LE, Zalom FG (1996) Ovipositional behavior and host discrimination in three scelionid egg parasitoids of stink bugs. Biological Control 6: 245–252. https://doi.org/10.1006/bcon.1996.0031

Wiedemann LM, Canto-Silva CR, Romanowski HP, Redaelli LR (2003) Oviposition behaviour of *Gryon gallardoi* (Hymenoptera.; Scelionidae) on eggs of *Spartocera dentiventris* (Hemiptera; Coreidae). Brazilian Journal of Biology 63: 781–785. https://doi.org/10.1590/S1519-69842003000100018

Zar JH (2010) Biostatistical Analysis, 5th Edn. Prentice Hall, Upper Saddle River, NJ, 555–565.

Zhang YZ, Li W, Huang, DW (2005) A Taxonomic study of Chinese species of *Ooencyrtus* (Insecta: Hymenoptera: Encyrtidae). Zoological Studies 44: 347–360.